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Pollen transport to *Lycium cooperi* (Solanaceae) flowers by flies and moths

William D. Wiesenborn*

Abstract.—*Lycium cooperi* (Solanaceae) is a woody shrub found along the eastern, northern, and western edges of the Mojave Desert in Arizona, Nevada, and California and along the western edge of the Sonoran Desert in California and Mexico. The plant produces funnel-shaped flowers during spring with stamens and a pistil that extend to near the top of a greenish-white corolla. I investigated the pollination of *L. cooperi* in southern Nevada during 30 March–21 April 2019 by aspirating insects from flowers, determining where they carried pollen on their bodies, and estimating the proportions of conspecific pollen in their pollen loads. Flowers were mostly visited at night by 8 species of moths (Lepidoptera) in Noctuidae and Geometridae and less frequently during the day by 3 species of flies (Diptera) in Syrphidae. The most frequent visitor to flowers was *Euxoa serricornis* (Noctuidae), followed by *Digrammia colorata* (Geometridae) and *Peridroma saucia* (Noctuidae), a widespread agricultural pest. Most flies at flowers were 2 large species of *Copestylum*. Flowers were also visited by the migratory butterfly *Vanessa cardui* (Lepidoptera: Nymphalidae). Pollen was carried mainly on the proboscis of moths and butterflies and on the anterior thorax of flies. *Lycium cooperi* pollen grains in brightfield microscopy are trilobed in polar view, elliptic in equatorial view, and grainy in appearance. A higher mean proportion of *L. cooperi* pollen was carried by moths and butterflies (0.50) compared with flies (0.21), and moths in Noctuidae carried a higher proportion of conspecific pollen (0.59) compared with moths in Geometridae (0.25). Insects pollinated only 19.8% of the profuse flowers produced by shrubs. Pollination of *L. cooperi* primarily by moths corresponds with the shrub's partially white and tubular flowers. Similar flowers on most other *Lycium* species in the Mojave and Sonoran Deserts indicate a likelihood of similar pollination by moths.

Resumen.—El *Lycium cooperi* (Solanaceae) es un arbusto leñoso que se encuentra a lo largo de los extremos este, norte y oeste del desierto de Mojave en Arizona, Nevada y California y a lo largo del extremo occidental del desierto de Sonora en California y México. Durante la primavera, la planta produce flores en forma de embudo con estambres y un pistilo que se extiende hasta cerca de la parte superior de una corola blanca verdosa. Durante marzo y abril de 2019 investigué la polinización de *L. cooperi* en el sur de Nevada. Para determinar en qué parte de sus cuerpos portan polen y estimar las proporciones de polen coespecífico en sus cargas de polen, recolecté insectos de las flores. Las flores fueron visitadas principalmente durante la noche por ocho especies de polillas (Lepidoptera) de Noctuidae y Geometridae, mientras que tres especies de moscas (Diptera) de Syrphidae lo hicieron con menor frecuencia durante el día. Los insectos que con mayor frecuencia visitaron las flores fueron las polillas *Euxoa serricornis* (Noctuidae), seguido de las *Digrammia colorata* (Geometridae) y de las *Peridroma saucia* (Noctuidae), que son una plaga agrícola muy extendida. La mayoría de las moscas en las flores pertenecían a dos especies grandes de *Copestylum*. Además, las flores fueron visitadas por la mariposa migratoria *Vanessa cardui* (Lepidoptera: Nymphalidae). El polen se transportó principalmente en la probóscide de las polillas y mariposas y en el tórax anterior de las moscas. Vistos bajo microscopio de campo claro, los granos de polen de *L. cooperi* se observan tri lobulados en una perspectiva polar y elípticos en una perspectiva ecuatorial, siendo su apariencia granulada. Las polillas y mariposas transportaron una mayor proporción promedio de polen de *L. cooperi* (0.50) en comparación con las moscas (0.21). Mientras que, las polillas Noctuidae portaron una proporción de polen coespecífico mayor (0.59) que las Geometridae (0.25). Los insectos polinizaron únicamente el 19.8% de las flores producidas por los arbustos. La polinización del arbusto leñoso *L. cooperi,* principalmente por parte de las polillas, se corresponde con las flores parcialmente blancas y tubulares de la especie. Las flores análogas en la mayoría de las otras especies de *Lycium,* en los desiertos de Mojave y Sonora, predicen polinizaciones similares a las polillas.

Lycium is a genus of thorny shrubs in Solanaceae that contains approximately 100 species disjointedly distributed in warm and dry regions of North and South America, southern Africa, Eurasia, and Australia (Fukuda et al. 2001, Nee 2012). *Lycium cooperi* A. Gray is a North American species that grows along the eastern, northern, and western margins of the Mojave Desert in Arizona, Nevada, and California and along the western margin of the Sonoran Desert in California and Mexico (Hitchcock 1932, Wiggins 1980, Benson and

*Corresponding author: wwiesenborn@fastmail.fm

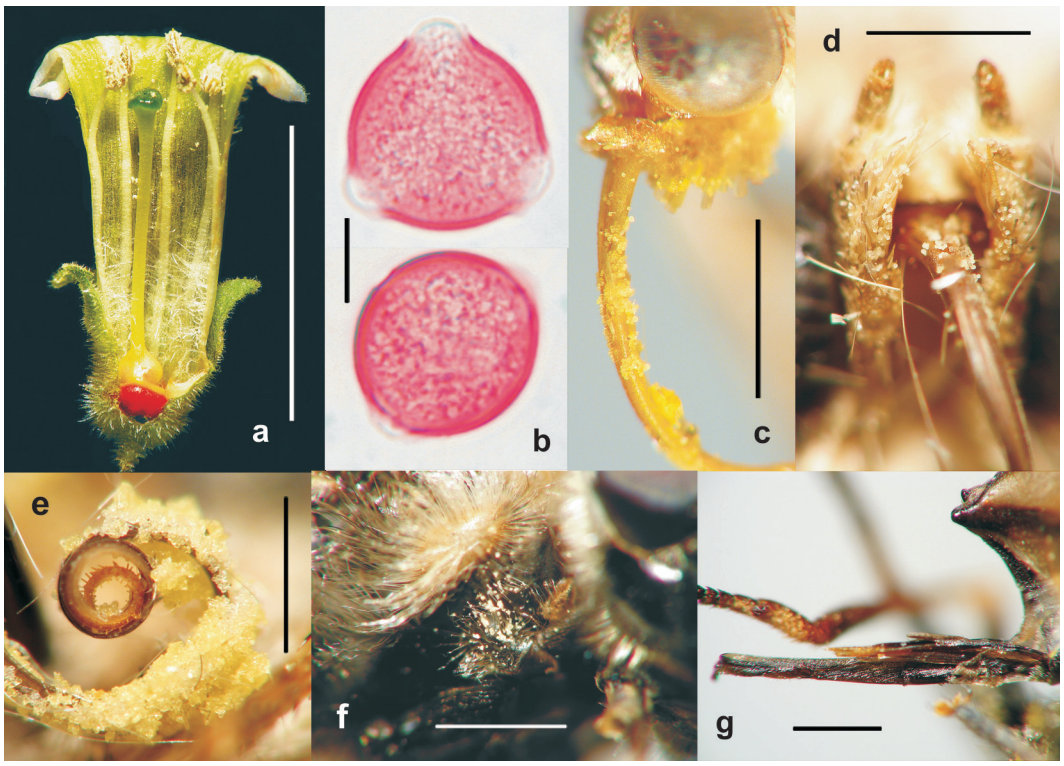

Fig. 1. Pollen on insects visiting *Lycium cooperi* flowers in southern Nevada during 30 March–21 April 2019. ***a,*** Side view of dissected flower. ***b,*** Stained pollen grains in polar (top) and equatorial (bottom) view. ***c,*** Proboscis and labial palps of *Digrammia colorata*. ***d,*** Labial palps of *Euxoa serricornis*. ***e,*** Proboscis of *Protogygia biclavis*. ***f,*** Proepimeron (at center) of *Copestylum fornax* (compound eye at upper right). ***g,*** Proboscis of *Copestylum isabellina*. Scale bar in panel *a* is 10 mm; scale bar in panel *b* is 10 μm; scale bars in panels *c*–*g* are 1 mm.

Darrow 1981). Plants grow to 2 m in height and width, produce dense foliage, and flower from March to May (Munz 1974). Flowers on *L. cooperi* (Fig. 1a) are abundant, clumped, and pendant with greenish-white corollas that are funnel shaped to cylindrical and 8–15 mm long (Chiang and Landrum 2009). Within flowers are 5 stamens with anthers at or just below the top of the corolla, a slightly lower 2-lobed stigma, and a superior ovary subtended by a circular nectary. Pollen grains from *Lycium* are tricolporate with the apertures at the equator and oblate-spheroidal to prolate-spheroidal in shape (Bernardello and Luján 1997, Perveen and Qaiser 2007). Fruits on *L. cooperi* are 5–10 mm long and contain 6–10 seeds (Chiang and Landrum 2009).

Pollination of *Lycium* has only been examined in South America. Galetto et al. (1998) examined the relationships between flower morphology, flower nectar composition, and taxa of flower visitors in 14 species of *Lycium* growing in temperate habitats in Argentina and Chile. The taxa of visitors were not influenced by the different sizes, shapes, and colors of flowers. The small amounts of nectar secreted by the nectary varied little in composition among species and also did not influence the taxa of flower visitors. Flowers were visited by a variety of insects including bees and wasps (Hymenoptera), flies (Diptera), and butterflies (Lepidoptera), except for one species visited by hummingbirds (Aves: Trochilidae).

In the present study, I investigated the pollination of *L. cooperi* in the Mojave Desert of southern Nevada by collecting insects on flowers and examining the locations and compositions of pollen loads. I examined the following questions: (1) What insects visit flowers and carry pollen? (2) Where do insects carry pollen on their bodies? And (3) how specific are the insects to *L. cooperi* flowers

based on the proportion of conspecific pollen in pollen loads?

METHODS

The study was conducted at 3 sites in the Eldorado Mountains in Clark County, southern Nevada. The lowest-elevation site (778 m; 35.716° N, 114.810° W) was 1.6 km northeast of Nelson. The site supported 3 clumped *L. cooperi* shrubs that were approximately 2 m in diameter and growing within a gravelly, southeast-trending wash. Plants were identified by referencing Chiang and Landrum (2009). Other *L. cooperi* at the site were uncommon, with the dominant vegetation comprising *Chrysothamnus* sp. (Asteraceae) and *Larrea tridentata* (DC) Coville (Zygophyllaceae). Plants that produced flowers in addition to *L. cooperi* included *Hymenoclea salsola* A. Gray (Asteraceae) and *Camissonia* sp. (Onagraceae). The middle-elevation site (860 m; 35.473° N, 114.842° W) was 7.1 km east of Searchlight. The site supported 11 scattered *L. cooperi* shrubs that were approximately 1.0–1.5 m in diameter and growing along a sandy, eastward-flowing wash. Other *L. cooperi* were uncommon, and dominant plants included *L. tridentata*, *H. salsola*, and *Ambrosia dumosa* (A. Gray) Payne (Asteraceae). Flowers were diverse but sparse and included *H. salsola*, *L. tridentata*, *Camissonia* sp., *Scutellaria mexicana* (Torrey) A.J. Paton (Lamiaceae), *Yucca schidigera* Ortgies (Asparagaceae), *Eriogonum* sp. (Polygonaceae), *Eriophyllum* sp. (Asteraceae), and *Amsinckia* sp. (Boraginaceae). The highest-elevation site (1028 m; 35.736° N, 114.830° W) was 3.1 km north of Nelson. The site supported 18 clumped *L. cooperi* shrubs that straddled a narrow wash and were 0.5–1.5 m in diameter. Other *L. cooperi* were uncommon, with the dominant plants comprising *L. tridentata*, *Prunus fasciculata* A. Gray (Rosaceae), *Gutierrezia* sp. (Asteraceae), and *Ephedra* sp. (Ephedraceae). Flowers were mostly *P. fasciculata*, *Camissonia* sp., *Ephedra* sp., *Amsinckia* sp., and sparse *Y. schidigera*. *Lycium andersonii* A. Gray also occurred in the area around the site but was less abundant, smaller, and was observed flowering earlier than *L. cooperii*. Rainfall at Searchlight during December 2018 through March 2019 totaled 100 mm (CCRFCD 2019), 115% of average rainfall during the same months in 1913–2016 (DRI 2019). I deposited a pressing (UNLV 66729) of flowering *L. cooperi* at the Wesley E. Niles Herbarium, University of Nevada, Las Vegas.

Flowers on *L. cooperi* shrubs were examined for insect visitors during 30 March–21 April 2019. Observations at each site started when shrubs began flowering and ended when flower corollas turned brown. Individual shrubs flowered for approximately 6 d. I examined flowers for 23.8 h during daytime (06:45–13:53 Pacific Daylight Time [PDT]) on 14 dates and for 23.5 h during dusk and nighttime (18:36–21:35 PDT) on 13 dates. Median times of sunrise and sunset were 06:14 PDT and 19:10 PDT. Flowers at night were illuminated with a flashlight covered with a red photographic filter. Insects landing on or next to flowers were aspirated through a tube into the top of a 125-mL plastic screw-capped flask, where they dropped individually into a 4-dram glass vial. I quickly killed each insect by temporarily inserting an ethyl acetate–saturated cotton applicator (attached to a cap) into the vial such that the applicator was situated above the insect. Two butterflies (Lepidoptera) that landed at flowers were captured with a net and killed by pinching their thoraxes. I recorded the time and air temperature when each insect was collected. Only trace amounts of rainfall occurred during the collection period.

Abundances of flowers on *L. cooperi* branches and their overall pollination rate were estimated. I flagged 4 branches on shrubs sampled for insects at each site when collecting ended, measured the length of the branch's main stem distal to the flag, and counted flowers on the main stem and lateral stems beyond the flag. The developing fruits (i.e., 4–6 mm in diameter and containing developing seeds) beyond each flag were counted 19–20 d later. Pollination rate was calculated from the total numbers of flowers and developing fruit.

The structure of *L. cooperi* pollen viewed in brightfield microscopy was determined by mounting pollen in polyvinyl alcohol (Dafni 1992). I vortexed flowers in 70% EtOH, centrifuged the suspended pollen at 3400 revolutions/min for 5 min, drew off the alcohol, and added 1 drop of 0.2% Safranin O stain in 25% EtOH. After 10 min, I added 4.0 mL of water, centrifuged the suspension again, drew off the water, added 0.6 mL of water, transferred the suspended pollen into a 35-mL porcelain

evaporating dish, and added 0.3 mL of a 12% solution of hydrolyzed polyvinyl alcohol. The mixture was vortexed and dried for 1.5 h at 45 °C to produce a 3.0-cm-diameter clear disk containing stained pollen. Pollen grains were photographed through a 100× oil-immersion objective lowered onto the disk and described following the terminology in Perveen and Qaiser (2007) and Punt et al. (2007). Following Punt et al. (2007), I measured the dimensions of pollen with an eyepiece reticle at 400×.

I determined the locations of pollen on the bodies of insects. Aspirated moths were pinned and their wings spread ventrum up, and flies were pinned dorsum up with the head unsupported to avoid disturbing the mouthparts and their pollen loads. Butterflies were pinned sideways. I examined each insect with a stereomicroscope and recorded the body structure with the highest, second highest, and third highest pollen density (number of pollen grains per body-structure area). Body structures followed Scott (1986) for moths and butterflies and McAlpine (1981), Vockeroth and Thompson (1987), and Krenn et al. (2005) for flies.

Proportions of pollen loads on insects made up of *L. cooperi* pollen grains were estimated in order to evaluate constancy to the species. Only insects that appeared to carry >15 grains were sampled. Pollen was removed from insects with a moistened 10/0 artist's brush, placed into 70% EtOH, vortexed to disperse the grains, and stained and mounted in polyvinyl alcohol. Disks containing pollen were compressed between 2 microscope slides and scanned at 100× with a mechanical stage on a compound microscope. Pollen was recognized by its staining and approximate symmetry. I categorized and counted pollen as *L. cooperi* or from a different species, with conspecific pollen recognized by its size, shape, and graininess. Pollen grains difficult to categorize were viewed at 200×. The disk was scanned either in its entirety or until >150 grains were categorized.

Insect species with >1 specimen were identified. I keyed moths to family with Borror et al. (1981) and identified species with Powell and Opler (2009) and the online photographs and distribution maps at Moth Photographers Group (2019). Butterflies were identified with Scott (1986). I compared moths and butterflies with specimens at the Entomology Research Museum, University of California, Riverside. Flies were keyed to genus with Vockeroth and Thompson (1987) and identified to species by comparing specimens with those in the collection. Vouchers of identified insects were deposited at the museum (UCRC-ENT 533376–99).

Locations of pollen on insects were ordered in each species. Body structures with pollen were ranked from 1 to 3 on each specimen in increasing order of pollen density. Ranks for each body structure were summed across specimens within each species to determine the structure with the highest, second highest, and third highest pollen density. Proportions of *L. cooperi* pollen in pollen loads were compared among species with >1 sampled insect with an analysis of variance (ANOVA in Systat version 10.2, Systat Software, Inc., https://systatsoftware.com). Proportions were transformed $2\arcsin(Y^{1/2})$ to normalize distributions and weighted by $1/s^2$ in each species to correct for unequal variances among species due to unequal pollen loads (Neter et al. 1996). Variation in proportions of conspecific pollen among species was decomposed into independent contrasts (Neter et al. 1996) in ANOVA that compared Lepidoptera versus Diptera, lepidopteran families Geometridae versus Noctuidae, noctuid genera *Euxoa* versus *Peridroma*, and dipteran (Syrphidae) genera *Copestylum* versus *Eupeodes*.

Results

Flowers on *L. cooperi* plants were profuse, appearing to nearly cover shrubs, but pollinated at a low rate. The 12 flagged branches totaled 340 cm in main-stem length and supported 1199 flowers on main and lateral stems. Flowers produced 237 developing fruit, with an estimated overall pollination rate of 19.8%. Flowers that I dissected under a microscope appeared to have high water contents by rapidly turning brown, especially the ovary when cut open. Some ovaries contained a larva that was keyed to Lepidoptera with Peterson (1962). Dissected flowers held only a small amount of nectar at the nectary. Attempts to measure nectar volume with micropipettes in the field during the evening yielded only trace amounts.

Pollen grains from *L. cooperi* flowers in brightfield microscopy (Fig. 1b) appear trilobed in polar view, with protruding apertures and rounded sides, and elliptic in equatorial view.

TABLE 1. Insects collected from *Lycium cooperi* flowers in southern Nevada and locations of pollen on their bodies.

Order[a], Family	Species	*n*	Collection time (PDT[b])	Collection temperature (°C)	Pollen locations on body: highest to lowest pollen density
L, Nymphalidae	*Vanessa cardui*	2	09:50–12:47	21–32	proboscis, eyes, frontoclypeus
L, Geometridae	*Archirhoe neomexicana*	3	20:07–20:57	10–12	proboscis, eyes, labial palps
	Digrammia colorata	18	19:00–20:55	6–24	proboscis, labial palps, ventral cavity[c]
	Plagiomimicus tepperi	2	19:45–20:29	10–22	proboscis, labial palps[d], ventral cavity[c,d], frontoclypeus[d]
L, Noctuidae	*Euxoa serricornis*	28	19:42–21:30	8–20	proboscis, labial palps, eyes
	Oxycnemis fusimacula	2	20:25–20:27	16–18	proboscis, ventral cavity[c], eyes
	Peridroma saucia	8	19:39–20:59	7–19	proboscis, antennae, labial palps[d], eyes[d]
	Protogygia biclavis	4	20:07–20:20	9–18	proboscis, labial palps, front tibiae
	Unciella primula	3	20:25–21:12	8–18	proboscis, labial palps, genae
D, Syrphidae	*Copestylum fornax*	6	08:20–13:31	16–31	proepimera, anepisterna, genae
	Copestylum isabellina	3	08:45–11:14	21–27	labium, prosternum, anepimera[d], front femora[d]
	Eupeodes volucris	4	08:08–13:27	15–33	postocular setae[d], anepisterna[d], katepisterna[d], anepimera[d]

[a]L = Lepidoptera; D = Diptera.
[b]PDT = Pacific Daylight Time.
[c]Between base of proboscis and bases of labial palps within cavity on ventral surface of head.
[d]Tied in rank.

Grains are oblate-spheroidal in shape, with the equatorial diameter ($\bar{x}$ = 25 μm, range 23–27 μm, n = 12) slightly greater than the polar axis ($\bar{x}$ = 22 μm, range 20–24 μm). Grains also have a distinctive, grainy appearance, suggesting a coarse, irregular exine.

I collected 95 insects from *L. cooperi* flowers and identified 83 insects in 12 species with >1 specimen. These included 1 species of butterfly in Nymphalidae, 8 species of moths in Geometridae and Noctuidae, and 3 species of flies in Syrphidae (Table 1). *Euxoa serricornis* (Smith) (Noctuidae) was the most frequently collected insect, followed by *Digrammia colorata* (Grote) (Geometridae). These 2 moths constituted most (55%) of the insects identified. The third most frequently collected insect was the large moth *Peridroma saucia* Hübner (Noctuidae), an agricultural pest with a wingspan of around 46 mm (Powell and Opler 2009). Moths collected in low numbers included the geometrids *Archirhoe neomexicana* (Hulst) and *Plagiomimicus tepperi* (Morrison) and the noctuids *Protogygia biclavis* (Grote), *Unciella primula* (Barnes & McDunnough), and *Oxycnemis fusimacula* Smith. Moths were collected from flowers as late as 21:30 PDT, 2.3 h after sunset, and at air temperatures as low as 6 °C (Table 1). The only butterfly collected was the painted lady, *Vanessa cardui* L. (Nymphalidae), a large species with a female forewing length of around 40 mm (Scott 1986). The 2 specimens were netted at different sites, and at one site the butterflies were seen stopping at *L. cooperi* flowers while migrating north in large numbers. Flies, all in Syrphidae, constituted only 16% of the insects identified. The large syrphids *Copestylum fornax* (Townsend) and *Copestylum isabellina* (Williston) were together most frequently collected, followed by the common *Eupeodes volucris* Osten Sacken. Flies were not collected until 08:08 PDT, when air temperature reached 15 °C (Table 1). Species with 1 specimen that were not identified included 10 moths (6 Noctuidae, 3 Geometridae, and 1 Pyralidae), 1 fly (*Copestylum* sp.), and 1 bee (*Lasioglossum* sp. in Halictidae). I also observed a few sphinx moths (Sphingidae) hovering at flowers during dusk and a few butterflies, other than *V. cardui*, landing at flowers during the day.

Pollen on moths and butterflies was carried primarily on the proboscis (Table 1; Fig. 1c, e). The labial palps held the second highest

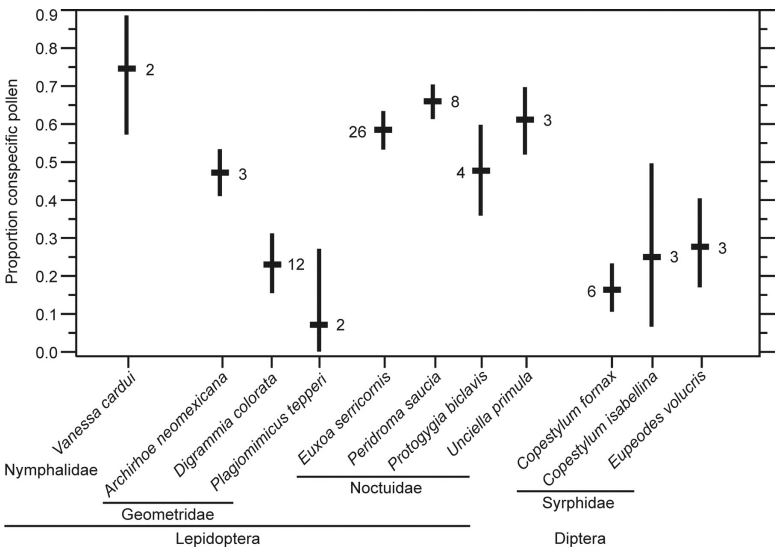

Fig. 2. Proportions of pollen load (±SE) composed of *Lycium cooperi* pollen on species with >1 sampled insect. Numbers of insects are next to the bars. Point estimates were back-transformed from data transformed 2 arcsin($Y^{1/2}$).

density of pollen (Fig. 1c, d). Pollen was also seen attached to hairs on the compound eyes of several species, and to the basal segments of the antennae on *P. saucia*. Two geometrid and one noctuid species carried pollen within the cavity at the ventrum of the head that is bounded laterally by the eyes. Pollen within the cavity accumulated between the base of the proboscis and the bases of the labial palps. The moth *P. tepperi* and the butterfly *V. cardui* carried significant amounts of pollen on the frontoclypeus at the front of the head.

Flies transported more pollen on the thorax than on the head (Table 1), in contrast to moths and butterflies. Pollen on syrphids was mostly on the anterior ventrum of the thorax on the proepimera (above the base of the front legs, Fig. 1f) and prosternum (at the base of the front legs), or on the sides of the thorax on the anepisterna (behind the posteriorly concave head). Pollen on the head accumulated on the genae above the mouth and on postocular setae behind the eyes. Only *C. isabellina*, the larger of the 2 *Copestylum* species, carried noticeable amounts of pollen on the mouthparts. Pollen on this species was attached mostly to the labium near the tip of the long foldable proboscis typical of the genus (Fig. 1g).

Specificities of insects visiting *L. cooperi* flowers varied among species based on proportions of conspecific pollen in pollen loads. Proportions of *L. cooperi* pollen on insects (n = 72) differed ($F_{10,61}$ = 5.45, P < 0.001) among the 11 species with >1 sampled insect (Fig. 2). Lepidoptera and Diptera carried different proportions of conspecific pollen ($F_{1,61}$ = 5.30, P = 0.025), with moths and butterflies carrying a higher proportion (0.50, back-transformed mean) than flies (0.21). Moths in Geometridae and Noctuidae also carried different proportions of *L. cooperi* pollen ($F_{1,61}$ = 11.4, P = 0.001), with noctuids carrying a higher proportion (0.59) than geometrids (0.25). Proportions of *L. cooperi* pollen on insects did not differ ($F_{1,61}$ = 1.18, P = 0.28) between the noctuids *E. serricornis* (0.59) and *P. saucia* (0.66). Proportions also did not differ ($F_{1,61}$ = 0.20, P = 0.66) between the 2 species of *Copestylum* (0.19) and *E. volucris* (0.28).

DISCUSSION

The copious flowers on *L. cooperi* shrubs were likely pollinated at a low rate due to the moderate numbers of insects observed to visit flowers. Flowers on shrubs were pollinated at one-third of the rate (59.9%) of bee-pollinated flowers on *L. tridentata*, or creosote bush (Boyd and Brum 1983), the most common shrub at the study sites. Visitation of *L. cooperi* flowers mostly by moths is consistent with floral structure and color. Moth-pollinated flowers tend

to be tubular in shape, corresponding with the long proboscis of Lepidoptera, and have whitish corollas that are more visually apparent at night (Willmer 2011). Pollination of *L. cooperi* by settling moths (i.e., species that land while probing for nectar) was enabled by the plant's dense foliage, which supported moths as they landed next to flowers. Pollination by moths is more common in warm desert regions such as the American Southwest (Willmer 2011). In the Mojave Desert, however, few species of plants have been reported to be moth-pollinated. Most studies have focused on the specialized pollination of monocot *Yucca* (Asparagaceae) plants by moths in Prodoxidae (Pellmyr and Segraves 2003, De la Rosa-Conroy et al. 2019).

Both species of moths that were most frequently collected, *E. serricornis* and *D. colorata*, are endemic to North American deserts. *Euxoa serricornis* inhabits the Mojave and Sonoran Deserts in southern California, southern Nevada, and southern Arizona (Lafontaine 1987). The reddish-orange forewings of the moths collected at *L. cooperi* flowers are characteristic of the species in Arizona (Lafontaine 1987). *Euxoa* larvae are commonly called cutworms and typically consume vegetation at the surface of the soil. Larvae of *E. serricornis* are unknown. Other larvae in the genus with known diets feed on a variety of plants while preferring those with broad leaves (Lafontaine 1987). *Digrammia colorata* feeds as larvae only on the leaves of *L. tridentata* (McFarland 1975, Rhoades 1977, as *Semiothisa colorata*). Creosote bush is a ubiquitous shrub in desert areas from southern California southeastward to southern Texas (Benson and Darrow 1981). *Peridroma saucia* is distributed worldwide and is most frequently found in weedy areas (Powell and Opler 2009). Larvae are known as variegated cutworms and feed on a wide variety of herbaceous plants including crops. The species is apparently native to Europe and was first recorded in North America in 1841 (Doane and Brodie 1901). The butterfly *V. cardui* is found nearly worldwide and develops as larvae on a wide range of plants (Scott 1986). The species occurs as a resident from the southern tip of Nevada southward and migrates north during spring to fall. Species and abundances of Lepidoptera that visit *L. cooperi* flowers likely vary across the plant's range due to different availabilities of host plants and across years due to differences in rainfall and temperature affecting population development.

The flies that visited *L. cooperi* flowers are detritivores or predators. Larvae of *Copestylum* eat decaying plant material, especially cacti (Vockeroth and Thompson 1987). *Copestylum fornax* has been found in the deserts of California and Baja California, Mexico, whereas *C. isabellina* has a more easterly distribution in the deserts of Arizona, New Mexico, and mainland Mexico (Cole 1969). Larvae of *E. volucris* eat aphids and are widespread across the western United States. (Essig 1926). Species and abundances of Diptera on *L. cooperi* flowers likely also vary geographically and temporally.

Moths and butterflies would have pollinated *L. cooperi* flowers while inserting their proboscises into the corolla and consuming nectar from the base of the ovary. The stamens and style of flowers pollinated by Lepidoptera typically extend to the top of the corolla, causing pollen to be transferred to the face or head and onto the stigma (Willmer 2011). Similarly, the position of the anthers at the top of the narrow corolla in *L. cooperi* flowers likely deposited pollen on the face and labial palps of the collected moths. The higher density of pollen on the proboscis was likely deposited when the proboscis was inserted and withdrawn from the flower. Pollination by the proboscis has been observed in Noctuidae and Geometridae that consume nectar at the bottom of the 15-mm-long tubular flowers on *Aspidosperma macrocarpon* Martius (Apocynaceae) trees in Brazil (Oliveira et al. 2004). The proboscis of moths feeding at *A. macrocarpon* flowers is forced between the anthers and along the slightly lower stigma at the midpoint of the corolla's length. Similar pollination occurs in *Aspidosperma tomentosum* Martius, a species with shorter (6-mm-long) corollas (Oliveira et al. 2004). Pollen on the proboscis of moths feeding at *L. cooperi* flowers would also have been more likely to reach the stigma due to its position below the anthers and the top of the corolla. Lepidoptera feeding at flowers would have obtained only a small amount of nectar. Flowers pollinated by settling moths usually contain low to moderate amounts of nectar (Willmer 2011), as observed in *A. macrocarpon* (Oliveira et al. 2004). Low rainfall prior to insects visiting plants (17 mm at Searchlight after 1 March 2019) may have

limited nectar production by the abundant flowers on *L. cooperi* shrubs. Movement by moths between flowers due to low nectar volume would have increased pollen transport between flowers on the same shrub or on different shrubs.

Flies appear to be less likely to pollinate flowers based on the locations of pollen on their bodies. Pollen would have been obtained by flies after they landed on the top of the corolla and fed on pollen or probed for nectar. Feeding by the 2 *Copestylum* species is likely similar to feeding by *Rhingia campestris* Meigen, a syrphid with similar mouthparts that feeds mostly on nectar (Krenn et al. 2005). Nectar is ingested by *R. campestris* with the narrow labellum at the tip of the proboscis beyond the labium (figs. 49–50 *in* Krenn et al. 2005). *Copestylum* flies would have contacted the anthers with their anterior thorax while inserting their proboscis into the corolla. Pollen on the thorax would be unlikely to be transferred to the stigma in most flowers. Pollen on the proboscis, observed in significant densities only on the labium of *C. isabellina*, may be able to reach the stigma and effect pollination. *Eupeodes volucris* contacted anthers but is less likely to reach the stigma in *L. cooperi* flowers due to its shorter mouthparts.

Greater specificity to *L. cooperi* flowers by Lepidoptera compared with Diptera is likely due to the correspondence between the plant's deep and narrow corollas and the long proboscis of moths and butterflies. Why moths in Noctuidae were more specific to *L. cooperi* than those in Geometridae is less clear. One explanation is the generally larger body size, and expectedly longer proboscis lengths, of noctuids. Flower constancies in moths tended to follow body size, because proportions of conspecific pollen were highest in the largest moth, *P. saucia*, and lowest in the smallest moth, *P. tepperi* (wingspan 30 mm, Powell and Opler 2009). This pattern also agrees with the highest floral constancy seen in the large butterfly *V. cardui*, an unexpected result given the species' migratory behavior. Lepidoptera with longer proboscises may be more capable of reaching nectar at the bottom of *L. cooperi*'s tubular corollas. Positive correlation between proboscis length and corolla length has been detected in a diversity of settling moths that visit flowers on xeric plants in Florida (Atwater 2013). Noctuids may also be less active fliers than geometrids, and less likely to visit flowers on other species, due to their larger bodies and higher wing loads (body mass–to–wing area ratio). The geometrid *D. colorata* was observed flying to flowers on other plant species during dusk. Specificity to the plant did not differ between the desert noctuid *E. serricornis* and the worldwide noctuid *P. saucia*. Specificity to *L. cooperi* by syrphids in *Copestylum* and *Eupeodes* also did not differ, despite their dissimilar mouthparts.

Insects collected from *L. cooperi* flowers differed greatly from those collected on various *Lycium* species in temperate habitats in Argentina and Chile (Galetto et al. 1998). Flowers in South America were visited mostly by Hymenoptera and Diptera, and Lepidoptera visited 47% of the species examined. All Lepidoptera on flowers were butterflies (mostly Nymphalidae) or skippers (Hesperiidae) except for Sphingidae, hovering moths that typically fly at dusk. Galetto et al. (1998) attributed visitation by butterflies but not moths to flowers secreting more nectar during the day than at night. Moth pollination has been observed in other genera of Solanaceae, but similar to *Lycium* in South America, the family does not generally exhibit a relationship between flower morphology and pollinator taxon (Knapp 2010). Exploitation of moths by *L. cooperi* for pollination may be due to its desert environment, which provides temperatures enabling flight activity during night (Willmer 2011).

Similar to *L. cooperi*, other desert species of *Lycium* in North America may rely on moths for pollination. In Arizona and California, all 10 of the other native *Lycium* species inhabit the Sonoran or Mojave Desert, and all but 2 of these (*L. parishii* and *L. torryi*) have funnel-shaped or tubular corollas that display white along with violet, lavender, purple, or green (Chiang and Landrum 2009, Nee 2012). Habitat and corolla shape and color predict that moths, and possibly butterflies, are important pollinators of these 8 species. Diptera and Hymenoptera may be more frequent visitors to flowers if the corolla displays a significant amount of violet or a similar color. Pollination of *Lycium* in North American deserts may have evolved in response to the region's abundant and diverse populations of moths.

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LITERATURE CITED

ATWATER, M.M. 2013. Diversity and nectar hosts of flower-settling moths within a Florida sandhill ecosystem. Journal of Natural History 47:2719–2734.

BENSON, L., AND R.A. DARROW. 1981. Trees and shrubs of the southwestern deserts. 3rd edition. University of Arizona Press, Tucson, AZ.

BERNARDELLO, L., AND M.C. LUJÁN. 1997. Pollen morphology of tribe Lycieae: *Grabowskia*, *Lycium*, *Phrodus* (Solanaceae). Review of Palaeobotany and Palynology 96:305–315.

BORROR, D.J., D.M. DE LONG, AND C.A. TRIPLEHORN. 1981. An introduction to the study of insects. 5th edition. Saunders College Publishing, Philadelphia, PA.

BOYD, R.S., AND G.D. BRUM. 1983. Predispersal reproductive attrition in a Mojave Desert population of *Larrea tridentata* (Zygophyllaceae). American Midland Naturalist 110:14–24.

CHIANG, F., AND L.R. LANDRUM. 2009. Vascular plants of Arizona: Solanaceae part three: *Lycium*. Canotia 5: 17–26.

[CCRFCD] CLARK COUNTY REGIONAL FLOOD CONTROL DISTRICT. 2019. Historical rainfall. Regional Flood Control District, Las Vegas, NV. http://gustfront.ccrfcd.org/rainfallSummary/default.aspx

COLE, F.R. 1969. The flies of western North America. University of California Press, Berkeley, CA.

DAFNI, A. 1992. Pollination ecology: a practical approach. IRL Press at Oxford University Press, Oxford, England, United Kingdom. 250 pp.

DE LA ROSA-CONROY, L., M.C. ARTEAGA, S.H. BULLOCK, L.E. EGUIARTE, AND R. BELLO-BEDOY. 2019. Population variation in the intensity of fruit infestation and pre-dispersal seed predation in *Yucca schidigera* (Asparagaceae) by its obligate pollinator. Plant Ecology 220:711–720.

[DRI] DESERT RESEARCH INSTITUTE. 2019. Cooperative climatological data summaries. Western Regional Climate Center, Reno, NV. https://wrcc.dri.edu/summary/Climsmaz.html

DOANE, R.W., AND D.A. BRODIE. 1901. The variegated cutworm. Washington Agricultural Experiment Station Bulletin 47:1–16.

ESSIG, E.O. 1926. Insects of western North America. The MacMillan Company, New York, NY.

FUKUDA, T., J. YOKOYAMA, AND H. OHASHI. 2001. Phylogeny and biogeography of the genus *Lycium* (Solanaceae): inferences from chloroplast DNA sequences. Molecular Phylogenetics and Evolution 19:246–258.

GALETTO, L., G. BERNARDELLO, AND C.A. SOSA. 1998. The relationship between floral nectar composition and visitors in *Lycium* (Solanaceae) from Argentina and Chile: what does it reflect? Flora 193:303–314.

HITCHCOCK, C.L. 1932. A monographic study of the genus *Lycium* of the Western Hemisphere. Annals of the Missouri Botanical Garden 19:179–374.

KNAPP, S. 2010. On 'various contrivances': pollination, phylogeny and flower form in the Solanaceae. Philosophical Transactions of the Royal Society B 365: 449–460.

KRENN, H.W., J.D. PLANT, AND N.U. SZUCSICH. 2005. Mouthparts of flower-visiting insects. Arthropod Structure and Development 34:1–40.

LAFONTAINE, J.D. 1987. Noctuoidea: Noctuidae (part): Noctuinae (part—*Euxoa*). The moths of America north of Mexico. Fascicle 27.2. Wedge Entomological Research Foundation, Washington, DC.

MCALPINE, J.F. 1981. Morphology and terminology—adults. Pages 9–63 *in* J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth, and D.M. Wood, coordinators, Manual of Nearctic Diptera. Volume 1. Agriculture Canada Monograph No. 27, Canadian Government Publishing Centre, Quebec, Canada.

MCFARLAND, N. 1975. Larval foodplant records for 106 species of North American moths. Journal of the Lepidopterists' Society 29:112–125.

MOTH PHOTOGRAPHERS GROUP. 2019. Mississippi Entomological Museum, Mississippi State University, Mississippi State, MS. https://mississippientomologicalmuseum.org.msstate.edu

MUNZ, P.A. 1974. A flora of Southern California. University of California Press, Berkeley, CA.

NEE, M.H. 2012. Solanaceae, nightshade family. Pages 1249–1258 *in* B.G. Baldwin, D.H. Goldman, D.J. Keil, R. Patterson, T.J. Rosatti, and D.H. Wilken, editors, The Jepson manual: vascular plants of California. 2nd edition. University of California Press, Berkeley, CA.

NETER, J., M.H. KUTNER, C.J. NACHTSHEIM, AND W. WASSERMAN. 1996. Applied linear statistical models. 4th edition. WCD McGraw-Hill, Boston, MA.

OLIVEIRA, P.E., P.E. GIBBS, AND A.A. BARBOSA. 2004. Moth pollination of woody species in the Cerrados of central Brazil: a case of so much owed to so few? Plant Systematics and Evolution 245:41–54.

PELLMYR, O., AND K.A. SEGRAVES. 2003. Pollinator divergence within an obligate mutualism: two yucca moth species (Lepidoptera; Prodoxidae: *Tegeticula*) on the Joshua tree (*Yucca brevifolia*; Agavaceae). Annals of the Entomological Society of America 96: 716–722.

PERVEEN, A., AND M. QAISER. 2007. Pollen morphology of family Solanaceae from Pakistan. Pakistan Journal of Botany 39:2243–2256.

PETERSON, A. 1962. Larvae of insects: an introduction to Nearctic species. Part I: Lepidoptera and plant infesting Hymenoptera. Edwards Brothers, Inc., Ann Arbor, MI.

POWELL, J.A., AND P.A. OPLER. 2009. Moths of western North America. University of California Press, Berkeley, CA. 369 pp.

PUNT, W., P.P. HOEN, S. BLACKMORE, S. NILSSON, AND A. LE THOMAS. 2007. Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology 143:1–81.

RHOADES, D.F. 1977. Integrated antiherbivore, antidesiccant and ultraviolet screening properties of creosotebush resin. Biochemical Systematics and Ecology 5: 281–290.

SCOTT, J.A. 1986. The butterflies of North America: a natural history and field guide. Stanford University Press, Stanford, CA.

Vockeroth, J.R., and F.C. Thompson. 1987. Syrphidae. Pages 713–743 *in* J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth, and D.M. Wood, coordinators, Manual of Nearctic Diptera. Volume 2. Agriculture Canada Monograph No. 28, Canadian Government Publishing Centre, Quebec.

Wiggins, I.L. 1980. Flora of Baja California. Stanford University Press, Stanford, CA.

Willmer, P. 2011. Pollination and floral ecology. Princeton University Press, Princeton, NJ.

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